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Identification and Delineation of Essential Habitat for Elasmobranchs in Estuaries on the Texas Coast

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Abstract

Essential habitat is required for a given species to complete its lifecycle and includes habitat for breeding, feeding, and growth. Estuaries provide essential habitat for many fishes, including elasmobranchs, particularly as nurseries. Shore-based, gillnet surveys have documented ten elasmobranch species (sharks and batoids) inhabiting Texas estuaries; however, limitations in the methodology, spatial, and temporal scope employed mean the role of these estuaries as elasmobranch nurseries remains uncertain. Therefore, an alternative sampling technique was implemented to survey open water locations in two Texas estuaries during the peak time of putative elasmobranch nursery usage (May to October). Ten species of elasmobranch were observed, including a shark, *Carcharhinus porosus*, and batoid species, *Hypanus americanus*, that were not documented in previous surveys. The most commonly encountered species, *Carcharhinus brevipinna*, comprised 45% of individuals caught, in contrast to previous surveys of these estuaries, in which the species was less than 1% of the total elasmobranch catch. The results revealed a distinction between sharks and batoids in terms of the life history stages present, as well as the depths and distances from the tidal inlet of areas in which they were encountered. Young-of-the-year and small juvenile *Carcharhinus brevipinna* and *Sphyrna lewini* were observed across multiple years and in multiple months within years at one site, suggesting that one of the sampled estuaries functions as a nursery. Although putative nurseries for these species have been identified elsewhere in the world, estuaries serving as nursery grounds in the western Gulf of Mexico are not well described.

Keywords Sharks · Batoids · Nursery habitat · Gulf of Mexico · Longline survey

Introduction

Habitat which is necessary for breeding, foraging, or growth of fishes is defined as essential fish habitat (EFH; Fluharty 2000). Estuaries are considered EFH for a variety of marine fishes (Beck et al. 2001), including elasmobranchs which use these habitats for fundamental processes such as feeding, mating, gestation, and parturition (Castro 1993; Tricas et al. 2000; Driggers et al. 2014). Estuaries are therefore commonly inhabited by elasmobranchs at a variety of life history stages, but estuarine habitat use varies among species. For example, species such as bonnethead sharks (*Sphyrna tiburo*), Atlantic stingrays (*Hypanus sabina*), and cownose rays (*Rhinoptera bonasus*) use estuaries throughout their life history (Snelson et al. 1988; Collins et al. 2007; Bethea et al. 2015). By contrast, many species included in the United States National Marine Fisheries Service (NMFS) large coastal shark management unit (e.g., blacktip sharks, *Carcharhinus limbatus*; spinner sharks, *Carcharhinus brevipinna*; bull sharks, *Carcharhinus leucas*; scalloped hammerhead sharks, *Sphyrna lewini*; NMFS, 2003) give birth in estuaries where young-of-the-year (YOY) and juveniles may remain for extended periods of time (Castro 1993; Simpfendorfer and Milward 1993; Heupel et al. 2004), but adults are mainly absent. An estuary can be defined as an elasmobranch nursery if YOY and juveniles (1) remain in or return to the estuary, (2) use the estuary repeatedly across years, and (3) are more common inside than outside the estuary (Heupel et al. 2007, 2019). To identify nurseries, sampling strategies which repeatedly capture YOY and juvenile elasmobranchs are necessary (Froeschke et al. 2010a). Consequently, delineating the range of species which use estuaries as EFH often requires long-term and diverse sampling strategies.

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In the northwestern Gulf of Mexico, a chain of barrier islands stretching approximately 600 km and punctuated by six major tidal inlets encloses temperate and subtropical estuaries along the coast of Texas, USA. These estuaries contain oyster reefs, seagrasses, and marshes that provide habitat for a variety of invertebrates, teleosts (Stunz et al. 2002, 2010), and at least ten species of elasmobranchs (Hueter and Tyminski 2007; Plumlee et al. 2018). Many of these estuaries are adjacent to large urban areas, increasing the potential for exploitation and habitat degradation. Elasmobranchs are particularly vulnerable to anthropogenic threats because of slow growth rates, late ages of reproductive maturity, and low fecundities relative to other marine fishes (Conrath and Musick 2012). Therefore, identification and delineation of elasmobranch EFH in these estuaries are crucial for management.

Long-term gillnet surveys carried out by Texas Parks and Wildlife Department (TPWD; Martinez-Andrade et al. 2012) have documented eight species of shark (including *S. tiburo*, *C. leucas*, *C. limbatus*, *C. brevipinna*, and *S. lewini*) and two species of batoid (*H. sabina* and *R. bonasus*) occupying Texas estuaries (Plumlee et al. 2018). The sampling strategy used by TPWD, however, may limit which species and life history stages are captured, because gillnets are deployed from shore in shallow water only and over two 10-week periods in April–June and September–November, excluding a period (July–August) of peak estuary usage for many coastal elasmobranchs in the northern Gulf of Mexico (May–October; Bethea et al. 2009). Further, the size selectivity of gillnets may preclude the capture of elasmobranchs larger than 2-m total length (Froeschke et al. 2010b) and limited data are available in the literature on the life history stage composition (i.e., YOY, juvenile, or mature) of species sampled (Plumlee et al. 2018).

In this study, demersal longlines were deployed monthly between May and November (spanning the periods covered by the more regular TPWD surveys), over 4 years to assess the diversity of elasmobranchs inhabiting three putative nursery sites in two Texas estuaries. Specifically, the objectives were to (i) compare elasmobranch community composition among sites; (ii) compare catch per unit effort of elasmobranch species and life history stages among sites; (iii) compare species-specific sex ratios; and (iv) determine environmental predicators of elasmobranch distribution.

Methods

Field Sampling

Three estuarine sites near Corpus Christi, TX, were each sampled on five occasions per year between May and November during 2015–2018. The initial intention was to sample each site once a month from May to September; however, sampling trips were sometimes rescheduled for logistical reasons. Numbered stations were created by drawing grids consisting of 64, 500-m × 500-m cells (16 km^2 in total) over each of three sites: Aransas Bay, Corpus Christi Bay, and Redfish Bay (Fig. 1). Each month, demersal longlines were deployed at one to four stations within each site, selected from grids using a random number draw between 1 and 64, without replacement. Longlines were 500 m in length and made from 4 mm 1200-lb. test monofilament line (Lindgren Pitman), with an anchor attached at each end. Demersal gangions were attached at 10-m intervals with buoys attached alongside the anchors and after every tenth gangion. Gangions measured approximately 3 m in length and consisted of 4 mm 1200-lb. test monofilament line, steel wire, and circle hooks (Mustad). On each longline, 40 gangions had 10/0 hooks and ten gangions had 15/0 hooks to allow for capture of YOY or juvenile and adult elasmobranchs, respectively. Each hook was baited with sectioned Atlantic mackerel (*Scomber scombrus*). In addition to longline deployments, a 100-m-long, 3.6-m-deep monofilament gillnet with 2-in. square mesh was deployed on seven occasions in Corpus Christi Bay in July 2017 and July and August 2018.

After deployment, latitude, longitude, water temperature, salinity, and dissolved oxygen were recorded at each location. Abiotic measurements were recorded using a YSI Pro 2030 instrument at the water surface and at the bottom or a depth of 3 m (here after referred to as surface and bottom, respectively). Longlines and gillnets were deployed for a minimum soak time of 60 min. Captured animals were brought aboard the vessel and the following data recorded: species, sex, life history stage (YOY, juvenile, mature), pre-caudal length (sharks

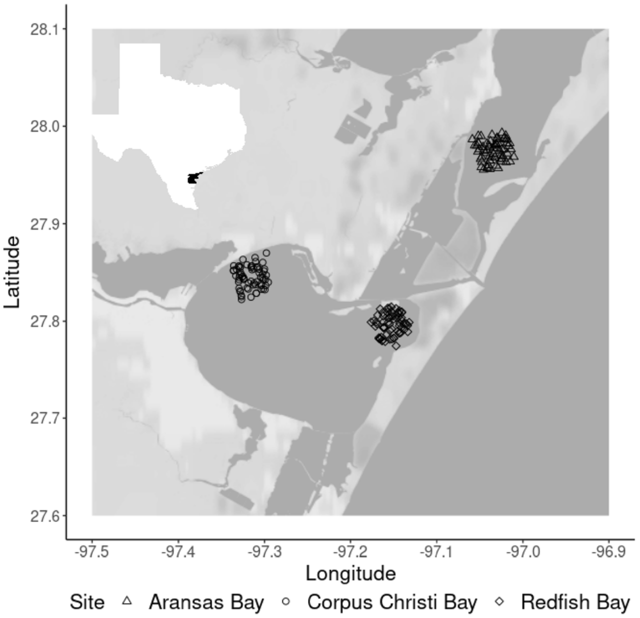

Fig. 1 Longline deployment locations at the three sites in Corpus Christi, TX, USA: Aransas Bay, Corpus Christi Bay, and Redfish Bay

only), fork length (sharks only), stretch total length (STL, sharks only), and disk width (batoids only). Life history stage for each elasmobranch was assessed on board the vessel using morphological characters: unhealed umbilical scars were used to identify YOY sharks (Duncan and Holland 2006) and presence of calcified claspers to confirm maturity in male elasmobranchs (Clark and von Schmidt 1965). In addition, a fin clip of approximately 1 cm^2 was collected from the trailing edge of the first dorsal fin of each shark or pelvic fin of each batoid and submerged in 20% DMSO-0.25M EDTA NaCl-saturated buffer (Seutin et al. 1991) for future genetic analysis. Each elasmobranch was dart tagged with a tag supplied by NMFS prior to being released. Each tag was individually coded and contained a telephone number for reporting recaptures to the NMFS laboratory in Panama City, FL, USA. Species identification was accomplished on board the vessel using morphological characteristics. For species which are sometimes misidentified in the field (i.e., *C. brevipinna*, *C. limbatus*, and Atlantic sharpnose shark *Rhizoprionodon terraenovae*), a section of the mitochondrial gene cytochrome c oxidase subunit I (CO1) was sequenced and used to confirm species identification in the field. If there was disagreement between species identification based on genetic analysis and observations in the field, genetic identification was used for downstream analysis.

Elasmobranch Data Analysis

All statistical analyses were conducted in R (R Development Core Team 2008) and an R Markdown document detailing all analyses is available at https://github.com/dgs108. To examine differences in elasmobranch communities among sites, the *adonis* function, available in the *vegan* package (Oksanen et al. 2018), was used, and degree of overlap in species composition between sites was determined using the Bray-Curtis dissimilarity statistic. To visualize differences in species composition among sites, non-metric multidimensional scaling (nMDS) was also executed.

Catch per unit effort (CPUE) was calculated for each longline deployment using the equation:

$$\mathrm{CPUE} = \frac{n}{\text{hook hours}}$$

where n is the number of elasmobranchs caught and hook hours is the number of hooks attached to the longline multiplied by the number of hours over which the longline was deployed.

To determine if there were differences in hook hours among sites and among months within sites, Kruskal-Wallis and Benjamini-Hochberg-corrected post hoc Dunn tests were used. Kruskal-Wallis and Benjamini-Hochberg-corrected post hoc Dunn tests also were also used to compare CPUE for elasmobranch species and life history stages among sites, as well as among months within sites. To test for differences in the frequencies of males and females for each elasmobranch species, chi-square tests were used. For situations in which life history stage could not be determined in the field, life history stage was estimated by comparing length measurements with species-specific age and growth data present in the literature (Branstetter and Stiles 1987; Snelson et al. 1988; Carlson and Parsons 1997; Carlson and Baremore 2003; Lombardi-Carlson et al. 2003; Carlson and Baremore 2005; Neer and Thompson 2005; Parsons and Hoffmayer 2007; Ramírez-Mosqueda et al. 2012).

Environmental Data Analysis

Geographic distance between each longline deployment location and the nearest tidal inlet was estimated using pairs of coordinates on the World Geodetic System ellipsoid (NIMA 2004) and the *pointDistance* function from the *raster* package (Hijmans 2017). These distances were corrected to exclude travel by land (i.e., "least-cost" distance) using the *gdistance* package (van Etten 2018). Water depth at each deployment location was estimated using bathymetry data from the National Oceanic and Atmospheric Administration (National Geophysical Data Center 2018). To examine differences in environmental variables (e.g., temperature, salinity, dissolved oxygen, depth, and distance from tidal inlet) among sites and on occasions when elasmobranch species were captured, Kruskal-Wallis tests were used and Benjamini-Hochberg-corrected post hoc Dunn tests were used to compare these variables between pairs of sites and species.

To determine the most influential environmental predictors of elasmobranch presence and abundance across all sites, boosted regression trees (BRTs) were executed. BRTs are a machine learning method which offers predictive advantages over generalized linear and additive models, particularly due to their relative insensitivity to multicollinearity and missing data (Breiman et al. 1984; Dormann et al. 2013). BRTs were executed using the *gbm.auto* package (Dedman et al. 2017) which implements a two-step (i.e., delta or hurdle) process to accommodate zero-inflated data which are characteristic of many elasmobranch catch datasets (Drymon et al. 2020). First, presence/absence was modelled using BRTs with a binary (Bernoulli) distribution, after which continuous non-zero abundance was modelled using BRTs with a Gaussian distribution. Tree complexity (tc), bag fraction (bf), and learning rate (lr) were optimized to achieve minimal predictive error and the optimal combination of these parameters was determined by selecting the model with the highest cross-validation (CV) score (Elith et al. 2008). Surface salinity, bottom salinity, surface temperature, bottom temperature, surface dissolved oxygen, bottom dissolved oxygen, depth, and distance from tidal inlet were modelled as explanatory variables in BRTs. Species-specific and batoid only datasets were too small to be modelled using BRTs; therefore, catch data for all large coastal shark species (i.e., *C. brevipinna*, *C. leucas*, *C. limbatus*, and *S. lewini*) were modelled together.

Results

Field Sampling

In total, 200 longlines were deployed between May 2015 and November 2018. In Corpus Christi Bay and Redfish Bay, 67 longlines were deployed, while 66 longlines were deployed in Aransas Bay; there were no differences in hook hours among sites or among months within sites (Fig. 2). Four sharks that were identified as *C. limbatus* in the field were identified as different species using CO1 sequence data: two *C. brevipinna*, one *R. terraenovae*, and one smalltail shark (*Carcharhinus porosus*). In addition, one shark identified as *C. brevipinna* in the field was identified as *R. terraenovae* using CO1 sequence data. Ten species of elasmobranch were caught during the sampling period. Five of these species belong to the family Carcharhinidae and two to the family Sphyrnidae. The other three species were batoids: southern stingray (*Hypanus americanus*), *H. sabina*, and *R. bonasus*. In total, 157 individual elasmobranchs were caught. *Carcharhinus brevipinna* was the most commonly caught elasmobranch, accounting for 45% of the total elasmobranch catch, and *S. tiburo* was the second most commonly caught elasmobranch, accounting for 22% of the total elasmobranch catch. Four elasmobranch species (*C. brevipinna*, *R. bonasus*, *S. lewini*, and *S. tiburo*) that were caught on longlines were also captured in gillnet deployments. Data collected from these gillnet deployments were not analyzed in conjunction with longline data.

Elasmobranch Community Composition

Three shark species, *C. leucas*, *C. brevipinna*, and *S. tiburo*, were caught in all three sites but were more common in Corpus Christi Bay (Table 1). *Rhizoprionodon terraenovae* was also caught in all three sites but was more common in Redfish Bay. *Carcharhinus porosus* and *S. lewini* were caught only in Corpus Christi Bay. By contrast, batoids were more common in Aransas Bay and Redfish Bay as compared with Corpus Christi Bay (Table 1). Elasmobranch community composition differed among sites ($p = 0.0040$, $R^2 = 0.0859$, Fig. 3) with 63% similarity in Corpus Christi Bay and Aransas Bay, 52% similarity in Aransas Bay and Redfish Bay, and 45% similarity in Corpus Christi Bay and Redfish Bay.

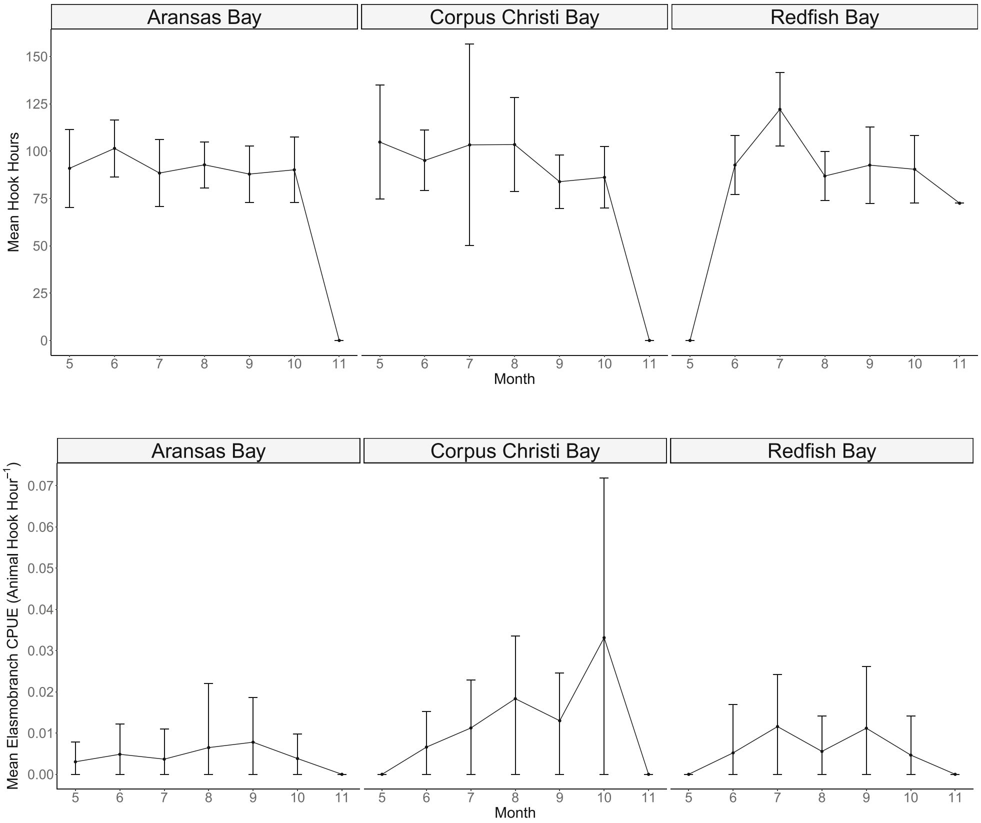

Fig. 2 Mean hook hours and catch per unit effort (CPUE) for all elasmobranchs by month in each site

Table 1 Elasmobranch abundance by site and life history stage. *YOY*, young-of-the-year; *JUV*, juvenile; *MAT*, mature; *UND*, undetermined

Species	Batoid or shark	Aransas Bay					Corpus Christi Bay					Redfish Bay				
		n	YOY	JUV	MAT	UND	n	YOY	JUV	MAT	UND	n	YOY	JUV	MAT	UND
Carcharhinus brevipinna	Shark	12	11	0	0	1	46	45	0	0	1	12	8	3	0	1
Carcharhinus leucas	Shark	3	1	2	0	0	4	4	0	0	0	1	0	1	0	0
Carcharhinus limbatus	Shark	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Carcharhinus porosus	Shark	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Rhizoprionodon terraenovae	Shark	1	1	0	0	0	5	5	0	0	0	8	8	0	0	0
Sphyrna lewini	Shark	0	0	0	0	0	4	1	3	0	0	0	0	0	0	0
Sphyrna tiburo	Shark	1	0	1	0	0	18	0	14	3	1	16	1	9	6	0
Hypanus americanus	Batoid	3	0	0	3	0	1	0	0	1	0	7	0	3	4	0
Hypanus sabina	Batoid	9	0	0	9	0	2	0	0	2	0	0	0	0	0	0
Rhinoptera bonasus	Batoid	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Elasmobranch CPUE Among Sites

Among sites, CPUE for all elasmobranchs varied ($p = 0.0021$, Fig. 2) and was greater in Corpus Christi Bay than Aransas Bay ($p = 0.0023$) and Redfish Bay ($p = 0.0154$). Species-specific CPUE varied among sites for *C. brevipinna*, *S. lewini*, *S. tiburo*, and *H. sabina* (Table 2). *Carcharhinus brevipinna* and *S. lewini* CPUE was greater in Corpus Christi Bay than Aransas Bay ($p = 0.0011$ and $p = 0.0213$, respectively) and Redfish Bay ($p = 0.0010$ and $p = 0.0415$, respectively), while *S. tiburo* CPUE was lower in Aransas Bay than Corpus Christi Bay ($p = 0.0049$) and Redfish Bay ($p = 0.0283$). By contrast, *H. sabina* CPUE was greater in Aransas Bay than Corpus Christi Bay ($p = 0.0217$) and Redfish Bay ($p = 0.0040$). CPUE also differed among months within sites for two species. *Carcharhinus brevipinna* CPUE in Corpus Christi Bay was greater in October than May ($p = 0.0407$) and *H. americanus* CPUE in Redfish Bay was greater in July than June ($p = 0.0133$), August ($p = 0.0143$), and October ($p = 0.0097$).

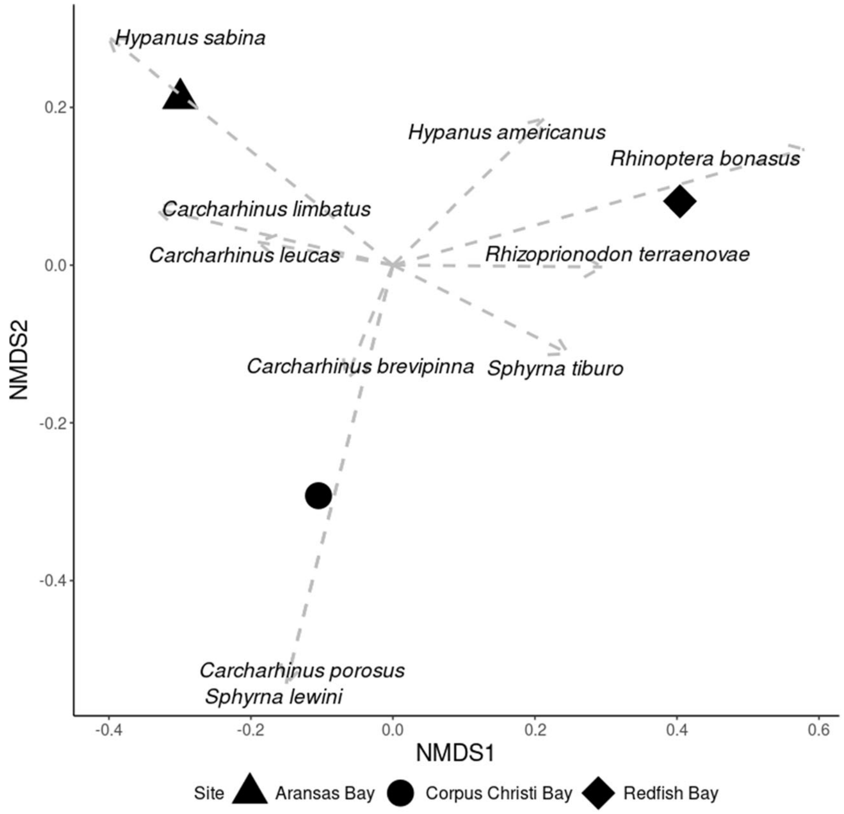

Fig. 3 Elasmobranch species composition among sites using non-metric multidimensional scaling

Table 2 Hook hours and species-specific catch per unit effort (per 1000 hook hours) by site. *C. bre*, *Carcharhinus brevipinna*; *C. leu*, *Carcharhinus leucas*; *C. lim*, *Carcharhinus limbatus*; *C. por*, *Carcharhinus porosus*; *R. ter*, *Rhizoprionodon terraenovae*; *S. lew*, *Sphyrna lewini*; *S. tib*, *Sphyrna tiburo*; *H. ame*, *Hypanus americanus*; *H. sab*, *Hypanus sabina*; *R. bon*, *Rhinoptera bonasus*

Site	Hook hours	*C. bre*	*C. leu*	*C. lim*	*C. por*	*R. ter*	*S. lew*	*S. tib*	*H. ame*	*H. sab*	*R. bon*
Aransas Bay	6015	1.91	0.49	0.14	0.00	0.14	0.00	0.22	0.49	1.50	0.00
Corpus Christi Bay	6452	7.88	0.52	0.18	0.15	0.90	0.50	2.96	0.14	0.29	0.00
Redfish Bay	6174	1.76	0.14	0.00	0.00	1.29	0.00	2.49	1.08	0.00	0.16
Total	18,641	3.76	0.50	0.11	0.05	0.75	0.21	1.90	0.59	0.59	0.05

Life History and Sex Differences

Across all sites, three distinct groups of species were evident based on life history stages present: *S. tiburo* was caught at all stages, 87% of batoids were mature, and, excluding *S. tiburo*, all sharks were YOY or juvenile. For all elasmobranch species, YOY CPUE was greater in Corpus Christi Bay than Aransas Bay ($p < 0.0001$) and Redfish Bay ($p < 0.0001$). A female-skewed sex ratio was observed across all sites for three species (Table 3): *H. sabina* (100% female, $\chi^2 = 11.0$, $p = 0.0009$), *H. americanus* (82% female, $\chi^2 = 4.5$, $p = 0.0348$), and *C. brevipinna* (67% female, $\chi^2 = 10.6$, $p = 0.0012$).

Environmental Predictors of Elasmobranch Distribution

Salinity ($p = 0.0022$), distance from tidal inlet ($p < 0.0001$), and depth ($p < 0.0001$) recorded at deployment locations varied among sites. Surface and bottom salinity were lower in Aransas Bay than Corpus Christi Bay ($p = 0.0055$ and $p = 0.0119$, respectively) and Redfish Bay ($p = 0.0010$ and $p = 0.0011$, respectively). Distance from tidal inlet and depth were both greater in Corpus Christi Bay than Aransas Bay ($p < 0.0001$) and Redfish Bay ($p < 0.0001$); distance from tidal inlet was shorter in Redfish Bay than Aransas Bay ($p < 0.0001$), but depth did not vary between these two sites. There was also variation in surface and bottom salinity ($p < 0.0001$) among the occasions when different species were caught (Table 4). *Carcharhinus brevipinna*, *S. lewini*, and *S. tiburo* were all caught at greater surface salinities than *H. americanus*, *H. sabina*, and *C. leucas* ($p < 0.03$). Furthermore, a distinction was observed in the distance from tidal inlet ($p = 0.0034$) and depth ($p = 0.0015$) of locations where sharks and batoids were caught. On average, batoids were caught in shallower water (3.55 m ± 0.48) at locations closer to the tidal inlet (18.27 km ± 5.21) as compared with sharks (3.97 m ± 0.58 and 24.54 km ± 7.50, respectively).

Abundance of all large coastal shark species (i.e., *C. brevipinna*, *C. leucas*, *C. limbatus*, and *S. lewini*) was modelled with BRTs to assess the environmental predictors of YOY and juvenile shark presence and

Table 3 Elasmobranch abundance by life history stage across all sites. The proportion of female individuals is given along with the chi-square statistic and associated *p* value

Species	Batoid or shark	n	YOY	JUV	MAT	UND	Proportion female	χ^2	*p* value
Carcharhinus brevipinna	Shark	70	64	3	0	3	0.671	9.94	0.0016
Carcharhinus leucas	Shark	8	5	3	0	0	0.750	2.00	0.1573
Carcharhinus limbatus	Shark	2	1	1	0	0	0.500	0.00	1.0000
Carcharhinus porosus	Shark	1	0	1	0	0	0.000	NA	NA
Rhizoprionodon terraenovae	Shark	14	14	0	0	0	0.429	0.08	0.7815
Sphyrna lewini	Shark	4	1	3	0	0	0.750	1.00	0.3173
Sphyrna tiburo	Shark	35	1	24	9	1	0.514	0.18	0.7316
Hypanus americanus	Batoid	11	0	3	8	0	0.818	4.50	0.0348
Hypanus sabina	Batoid	11	0	0	11	0	1.000	11.0	0.0009
Rhinoptera bonasus	Batoid	1	0	0	1	0	1.000	NA	NA

Table 4 Mean (± standard error) environmental conditions at which each species was caught

Species	S.Temp. (°C)	B.Temp. (°C)	S.Sal.	B.Sal.	S.DO (mg L^{-1})	B.DO (mg L^{-1})	Dist. (km)	Depth (m)
Carcharhinus brevipinna	29.5 ± 1.63	29.3 ± 1.53	31.7 ± 3.60	32.3 ± 3.58	5.87 ± 0.53	5.57 ± 0.57	25.6 ± 7.15	4.02 ± 0.57
Carcharhinus leucas	29.3 ± 1.58	30.0 ± 1.82	22.9 ± 6.40	28.7 ± 2.34	6.14 ± 0.52	5.05 ± 1.38	24.5 ± 6.81	3.81 ± 0.44
Carcharhinus limbatus	29.9 ± 0.50	30.1 ± 0.78	25.4 ± 2.97	29.4 ± 1.41	5.83 ± 0.03	5.25 ± 0.12	24.9 ± 8.17	4.03 ± 0.86
Carcharhinus porosus	29.5 ± NA	29.5 ± NA	24.0 ± NA	32.4 ± NA	NA	NA	29.3 ± NA	4.40 ± NA
Rhizoprionodon terraenovae	30.5 ± 0.73	30.1 ± 0.60	30.1 ± 3.56	31.4 ± 3.10	5.82 ± 0.34	5.17 ± 0.55	20.8 ± 7.62	3.89 ± 0.60
Sphyrna lewini	30.1 ± 1.21	29.9 ± 1.24	35.2 ± 3.96	35.4 ± 3.84	5.62 ± 0.54	5.42 ± 0.47	30.6 ± 1.30	4.48 ± 0.15
Sphyrna tiburo	30.3 ± 1.13	29.9 ± 0.92	33.1 ± 3.02	34.9 ± 3.35	5.55 ± 0.56	5.31 ± 0.53	23.1 ± 8.20	3.85 ± 0.63
Hypanus americanus	29.6 ± 1.95	28.8 ± 1.21	28.5 ± 3.64	31.0 ± 3.05	6.25 ± 0.70	5.53 ± 0.49	16.8 ± 4.32	3.60 ± 0.42
Hypanus sabina	28.8 ± 3.01	28.8 ± 2.91	23.7 ± 5.97	25.3 ± 5.90	6.16 ± 0.81	5.45 ± 0.84	20.2 ± 5.62	3.61 ± 0.40
Rhinoptera bonasus	29.7 ± NA	29.4 ± NA	34.6 ± NA	34.7 ± NA	5.44 ± NA	5.52 ± NA	12.7 ± NA	2.33 ± NA

S.Temp., surface temperature; *B.Temp.*, bottom temperature; *S.Sal.*, surface salinity; *B.Sal*, bottom salinity; *S.DO*, surface dissolved oxygen; *B.DO*, bottom dissolved oxygen; *Dist.*, distance from tidal inlet

abundance across all sites. Based on the highest model CV scores (0.8048 for binary and 0.7127 for Gaussian), the optimum parameters for the binary BRTs were tc = 8, bf = 0.7, and lr = 0.0027; the optimum parameters for the Gaussian BRTs were tc = 8, bf = 0.7, and lr = 0.0037. The most influential predicators of shark presence were distance from tidal inlet (20.6%) and depth (14.9%), while surface salinity (59.8%) was the most influential predictor of shark abundance (Table 5).

Discussion

Assessing Elasmobranch Communities

The diversity of elasmobranch species observed in this study was comparable with that documented by other studies of Gulf of Mexico estuaries (Wiley and Simpfendorfer 2007; Bethea et al. 2009; Drymon et al. 2010; Bethea et al. 2015; Plumlee et al. 2018), and eight of the species observed in this study were previously observed during TPWD's gillnet surveys (Plumlee et al. 2018). However, two additional species were observed in this study that were not in the TPWD dataset: *H. americanus*, caught on multiple occasions during this study, and *C. porosus*, caught once. *Carcharhinus porosus* is a small coastal carcharhinid that occurs in warm waters of the western Atlantic Ocean, including the Gulf of Mexico, and Corpus Christi Bay is considered to be near the northern limit of its range (McEachran and Fechhelm 2005). The observation of *C. porosus* in this study is only the second verified observation in Texas (Hendrickson and Cohen 2015) and whether the species is an occasional vagrant or a misidentified component of the coastal fish fauna of South Texas will require further study. Additionally, there were differences in relative abundance of specific species between this study and those based on the TPWD dataset (Plumlee et al. 2018). *Carcharhinus leucas*, one of the most abundant elasmobranchs found in Corpus Christi Bay and Aransas Bay during TPWD surveys (22.3%), only represented 5.1% of elasmobranch catch in this study. By contrast, *C. brevipinna*,

Table 5 Relative influence of environmental variables on large coastal shark presence (binary) and abundance (Gaussian)

Best binary BRT variables	Relative influence (binary)	Best Gaussian BRT variables	Relative influence (Gaussian)
Distance from tidal inlet	20.6	Surface salinity	59.8
Depth	14.9	Surface temperature	11.7
Surface dissolve oxygen	12.3	Surface dissolve oxygen	7.0
Bottom dissolve oxygen	11.4	Bottom salinity	6.8
Surface temperature	11.1	Depth	4.9
Bottom temperature	10.3	Bottom dissolve oxygen	3.6
Surface salinity	10.0	Distance from tidal inlet	3.5
Bottom salinity	9.5	Bottom temperature	2.7

the most commonly caught species during this study, was more than an order of magnitude more common than *C. limbatus*, while *C. limbatus* was more than ten times more common than *C. brevipinna* in TPWD data.

Discrepancies in the diversity and abundance of elasmobranchs between our study and previous surveys of these estuaries are likely because of differences in sampling method, location, and timing. TPWD's gillnet survey is conducted April–June and September–November (Martinez-Andrade et al. 2012) with gillnets deployed from shore. Gillnet sampling can limit the capture of larger elasmobranchs (i.e., sharks greater than 2-m STL, Froeschke et al. 2010b), as well as large batoids like *H. americanus*; thus, gear bias may explain why this species was not previously documented. The nearshore habitat sampled by TPWD includes shallow creeks with salinity regimes (7–20) preferred by small *C. leucas* individuals (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008) but out of the range of salinity preferred by more stenohaline species. In this study, gear was deployed farther from shore and salinities 7–20 were recorded on only 5% of longline deployments, suggesting that this survey did not likely sample in ideal juvenile *C. leucas* habitat. Previous research suggests that *C. brevipinna* juveniles prefer deeper habitat as compared with *C. limbatus* (Ward-Paige et al. 2015); therefore, spatial differences in sampling stations could explain the discrepancy in abundances of these two species between the surveys.

Elasmobranch Diversity, Life History Composition, and Sex Ratios

Sphyrna tiburo represented a large proportion of the total elasmobranch catch in this study (22%). This species was unique in this study because all life history stages were found in moderately saline (33.1 ± 3.02) estuarine habitat. This observation is consistent with studies in the eastern Gulf of Mexico (Ward-Paige et al. 2015), Southeastern USA (Ulrich et al. 2007; McCallister et al. 2013), and Brazil (Lessa and Almeida 1998). The reproductive strategy of *S. tiburo* is distinct from large coastal shark species because females do not use estuaries for parturition (Ulrich et al. 2007; Driggers et al. 2014). Instead, female *S. tiburo* are thought to migrate into estuaries in the spring to decrease the gestational period (4 to 5 months; Manire et al. 1995) by feeding on high energy prey items, particularly crabs in the genus *Callinectes* (Cortés et al. 1996; Lessa and Almeida 1998; Plumlee and Wells 2016). In the late summer, *S. tiburo* females move offshore for parturition and mating (Driggers et al. 2014). Three mature female and six mature male *S. tiburo* were encountered, suggesting males also enter estuaries prior to mating. Only one YOY *S. tiburo* was caught on longline deployments compared with 25 juveniles, but YOY *S. tiburo* individuals may be too small to be caught frequently on 10/0 hooks. In addition, YOY *S. tiburo* individuals have previously been sampled close to shore in Corpus Christi Bay and Aransas Bay using gillnets (Plumlee et al. 2018). This suggests that YOY *S. tiburo* may disperse into estuaries after parturition and remain close to shore, potentially to avoid predation by older juveniles of large coastal shark species that occupy deeper waters.

For all other shark species (excluding *S. tiburo*), only YOY and juveniles were observed, despite the use of 15/0 hooks meant to target adult individuals. The majority of sharks (59%) were observed in Corpus Christi Bay and only one shark species (*R. terraenovae*) was observed in greater abundance in another site (Redfish Bay). *Rhizoprionodon terraenovae* females mate and give birth offshore with YOY immediately dispersing into estuaries (Parsons and Hoffmayer 2005). Juveniles of this species do not remain in estuaries but utilize a series of coastal habitats (Carlson et al. 2008) and this likely explains why only YOY *R. terraenovae* individuals were observed and in greatest abundance in Redfish Bay, which is close to the tidal inlet. By contrast, YOY and juveniles of the large coastal shark species *C. brevipinna*, *C. limbatus*, *C. leucas*, and *S. lewini* were predominantly observed in Corpus Christi Bay (65%), and these species exhibit a similar reproductive strategy. Females migrate into or near estuaries for parturition and are thought to leave these habitats shortly after giving birth (Castro 1993; Holland et al. 1993; Simpfendorfer and Milward 1993). The largest animal observed in this study was a juvenile *C. leucas* measuring < 1500-mm STL, suggesting larger sharks do not frequently inhabit the areas of estuaries sampled during the time period in which gear was deployed.

Unlike sharks, batoids observed in this study were predominantly mature females. *Hypanus americanus* and *H. sabina* are known to use estuaries for parturition (Johnson and Snelson 1996; Gelsleichter et al. 2006; Yokota and Rosângela 2006) which likely explains the female-skewed sex ratios observed for both species. In addition to parturition, dasyatid species such as *H. sabina* and *H. americanus* mate in shallow coastal habitats in the eastern Gulf of Mexico (Johnson and Snelson 1996; Tricas et al. 2000), Bahamas (Chapman et al. 2003), and southeastern Australia (Pierce et al. 2009). *Hypanus americanus* females become receptive to mating immediately after giving birth (Chapman et al. 2003) and in this study, mature *H. americanus* males were observed twice on the same days and in the same areas as mature females. *Hypanus americanus* CPUE was greatest in July, perhaps indicating the peak period of estuary use for this species. The three batoid species observed in this study are commonly found in shallow water near to shore (McEachran and Fechhelm 2005), but *R. bonasus* and *H. americanus* are also encountered offshore (Ajemian and Powers 2016; Last et al. 2016). The capture of these two species close to the tidal inlet may also reflect their movement into and out of these estuaries. *Hypanus sabina* is a euryhaline species (Snelson et al. 1988; Johnson and Snelson 1996) and we found the greatest *H. sabina* CPUE in Aransas Bay, which was the site with the lowest salinity and lowest shark abundance. This suggests that in these estuaries, *H. sabina* may prefer habitats with lower salinities, potentially to avoid predation by more stenohaline sharks.

In addition to batoids, a female-skewed sex ratio was observed for juvenile/YOY *C. brevipinna* which could be explained by several reasons: (1) males experience higher mortality than females, (2) litters are skewed in favor of females, and/or (3) behavioral traits resulted in more females being caught than males. Selective mortality of male *C. brevipinna* seems unlikely, and studies of the species elsewhere have documented even sex ratios in litters (Allen and Cliff 2000; Capapé et al. 2003; Joung et al. 2005). Although sex ratios of *C. brevipinna* litters in the western Gulf of Mexico have not been assessed, even sex ratios at birth are a consistent observation across live-bearing sharks (Stevens and McLoughlin 1991; Henderson et al. 2009). Therefore, sexual segregation and aggregation of females in the sampled habitat seem like the most likely explanation. Sexual segregation in sharks is well documented, particularly in large coastal sharks (Klimley 1987; Economakis and Lobel 1998; Sims 2005; Nosal et al. 2013), but the behavior is usually associated with adult females avoiding harassment by males attempting to copulate and is thus seen in later life stages. Differences in migratory behavior between sexes have been observed in large juvenile sandbar sharks (*Carcharhinus plumbeus*; Grubbs et al. 2007) but sexual segregation of small juveniles and YOY in an estuary would be a novel observation, although further research is required to verify this.

Environmental Predictors of Large Coastal Shark Presence/Abundance

Across all sites, the presence of YOY and juveniles of large coastal shark species increased as the distance from tidal inlet (> 19 km) and depth (> 3.6 m) of deployment locations increased. On average, habitats sampled in Corpus Christi Bay were deeper (4.3 m ± 0.28) and farther from the tidal inlet (30.7 km ± 1.3), as compared with both Aransas Bay (3.5 m ± 0.19 and 18.3 km ± 1.26, respectively) and Redfish Bay (3.3 m ± 0.47 and 13.7 km ± 1.27, respectively). CPUE for all elasmobranchs was greatest in Corpus Christi Bay and 67% of all elasmobranchs caught there were YOY/juveniles of large coastal shark species. Moderately deep habitats farther from areas that potential predators (i.e., adults of large coastal shark species) are likely to inhabit could provide better refuge for YOY and juvenile sharks, and this likely explains the greater abundance of these smaller individuals (i.e., YOY/juveniles of large coastal shark species) caught in Corpus Christi Bay. Preference for habitats that are relatively distant from offshore areas by YOY and juvenile sharks has also been observed in estuaries of the eastern Gulf of Mexico (Ward-Paige et al. 2015), the Atlantic Coast of the USA (Conrath and Musick 2007), and the eastern coast of Australia (Yates et al. 2015). Furthermore, multiple studies have demonstrated that YOY and juvenile sharks occupy habitats which confer reduced predation risk but move in this habitat as physical characteristics like depth and salinity change (Conrath and Musick 2007; Heupel and Simpfendorfer 2011; Guttridge et al. 2012). Although adult sharks that prey upon YOY and small juvenile sharks can enter Corpus Christi Bay, the distance between this site and offshore areas likely decreases the risk of predation and results in greater abundance of YOY and small juveniles.

Surface salinity (> 30) was the best predictor of large coastal shark species abundance across all sites. The lowest abundance of large coastal sharks was in Aransas Bay and this site also had the lowest average surface salinity (27.8 ± 6.76). Salinities greater than 30 have been linked to increased abundance of large coastal sharks in other Gulf of Mexico estuaries (Froeschke et al. 2010b; Ward-Paige et al. 2015; Plumlee et al. 2018) with the exception of *C. leucas*, which prefers low to moderate salinities (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008) and was rarely observed in this study. Therefore, the greater abundance of large coastal sharks in Corpus Christi Bay may also be a consequence of the salinities preferred by relatively stenohaline *C. brevipinna*, *C. limbatus*, and *S. lewini*.

Shark Nurseries

In addition to individuals caught on longlines, nine *S. lewini* and seven *C. brevipinna* were caught in gillnets in Corpus Christi Bay. Combined with the longline data, both species were caught in Corpus Christi Bay across months within years and repeatedly across years, suggesting this estuary may act as nursery habitat for both, following Heupel et al. (2007). Establishing whether density in the putative nursery is greater than other areas requires additional sampling outside the estuary using similar methods at similar times of year. Additionally, acoustic telemetry could be used to track the movement of juveniles and compare time spent inside and outside of the estuary. Environmental conditions observed in Corpus Christi Bay resemble those of *S. lewini* and *C. brevipinna* nurseries identified outside of the Gulf of Mexico. Putative *S. lewini* nurseries with high salinities (28–35) and shallow depths (< 5 m) have been described in northeastern Australia (Simpfendorfer and Milward 1993), Hawaii (Duncan and Holland 2006), and along the southeastern coast of the USA (Castro 1993). Moderately shallow (< 12 m) habitats across a range of salinities (28–42) have been identified as putative *C. brevipinna* nurseries in Western Australia (White and Potter 2004) and off the coast of the Carolinas, USA (Castro 1993; Thorpe et al. 2004).

Both *C. brevipinna* and *S. lewini* were observed in October, and the greatest CPUE for *C. brevipinna* occurred during that month. In coastal waters of the Carolinas, juveniles of both species are found from May to September, with an estimated thermal tolerance between 17 and 31 °C (Ulrich et al. 2007). In North Carolina, USA, *C. brevipinna* abundance peaks in September (Thorpe et al. 2004), while in the eastern Gulf, abundance peaks in September–November (Drymon et al. 2010). In South Carolina, USA, juvenile *S. lewini* leave estuaries in September (Ulrich et al. 2007). Elsewhere in the world, juveniles of large coastal shark species (e.g., *C. limbatus* and *C. leucas*) have been documented to be year-round residents of estuaries when temperatures remain relatively stable throughout the year (Simpfendorfer and Milward 1993; Wiley and Simpfendorfer 2007). Therefore, it is likely that Corpus Christi Bay would be suitable habitat for *C. brevipinna* and *S. lewini* for most of the year, except between late December to February when temperatures are below 17 °C (Applebaum et al. 2005). Further research is required to determine at which point YOY and juvenile sharks leave estuaries in the northwestern Gulf.

Conclusions

With the mandate to incorporate essential fish habitat into fisheries management plans, identification of critical habitats in estuaries has gained importance. This study identifies essential habitat for multiple species of elasmobranch and delineates distinct areas used by sharks and batoids. *Sphyrna tiburo* occupied moderately saline estuarine habitat at all life history stages. Batoids were predominantly mature females and more frequently found in shallower habitat closer to the tidal inlet. Two batoid species, *H. americanus* and *H. sabina*, appear to be using these estuaries for mating and parturition. By contrast, YOY and juvenile sharks, primarily large coastal species, were found to prefer deeper and more saline habitat farther from the tidal inlet. This preference is likely based on the decreased risk of predation from larger sharks which primarily occur offshore. The ability of specific species to tolerate fresh water likely mediates habitat use and *Carcharhinus leucas*, which prefer relatively freshwater as juveniles, was distinct from the other large coastal shark species because it was found in less saline conditions. In addition, results of this study indicate that Corpus Christi Bay may be a nursery for *C. brevipinna* and *S. lewini*; however, further research is required for a formal designation.

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References

Ajemian, M.J., and S.P. Powers. 2016. Seasonality and ontogenetic habitat partitioning of cownose rays in the northern Gulf of Mexico. *Estuaries and Coasts* 39 (4): 1234–1248. https://doi.org/10.1007/s12237-015-0052-2.

Allen, B., and G. Cliff. 2000. Sharks caught in the protective gill nets of Kwazulu-Natal, South Africa. The spinner shark *Carcharhinus brevipinna*. *South African Journal of Marine Science* 22 (1): 199–215.

Applebaum, S., P.A. Montagna, and C. Ritter. 2005. Status and trends of dissolved oxygen in Corpus Christi Bay, Texas, U.S.A. *Environmental Monitoring and Assessment* 107 (1-3): 297–311. https://doi.org/10.1007/s10661-005-3111-5.

Beck, M.W., K.L. Heck, K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51 (8): 633–641.

Bethea, D.M., L. Hollensead, J.K. Carlson, M.J. Ajemian, R.D. Grubbs, E.R. Hoffmayer, R. Del Rio, G.W. Peterson, D.M. Baltz, and J. Romine. 2009. Shark nursery grounds and essential fish habitat studies: Gulfspan Gulf of Mexico FY'08 - cooperative Gulf of Mexico states shark pupping and nursery survey. In *Contribution Report PCB-08/02 to the National Oceanic and Atmospheric Administration*. RI, USA.: Narragansett.

Bethea, D.M., M.J. Ajemian, J.K. Carlson, E.R. Hoffmayer, J.L. Imhoff, R.D. Grubbs, C.T. Peterson, and G.H. Burgess. 2015. Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. *Environmental Biology of Fishes* 98 (5): 1233–1254. https://doi.org/10.1007/s10641-014-0355-3.

Branstetter, S., and R. Stiles. 1987. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. *Environmental Biology of Fishes* 20 (3): 169–181.

Breiman, L., J.H. Friedman, R.A. Olshen, and C.J. Stone. 1984. *Classification and regression trees*. Belmont: Wadsworth International Group.

Capapé, C., A. Abdoulaye Seck, Y. Diatta, C. Youssouph Diatta, J. Zaouali, and F. Hemida. 2003. Distribution and reproductive biology of the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1841) (Chondrichthyes: Carcharhinidae). *Israel Journal of Zoology* 49: 269–286.

Carlson, J.K., and I.E. Baremore. 2003. Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? *Marine & Freshwater Research* 54 (3): 227–234. https://doi.org/10.1071/MF02153.

Carlson, J.K., and I.E. Baremore. 2005. Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and

Gulf of Mexico coasts: a comparison of methods. *Fishery Bulletin* 103: 280–291.

Carlson, J.K., and G.R. Parsons. 1997. Age and growth of the bonnethead shark, *Sphyrna tiburo*, from Northwest Florida, with comments on clinal variation. *Environmental Biology of Fishes* 50 (3): 331–341.

Carlson, J.K., M.R. Heupel, D.M. Bethea, and L.D. Hollensead. 2008. Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). *Estuaries and Coasts* 31 (5): 931–940. https://doi.org/10.1007/s12237-008-9075-2.

Castro, J.I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes* 38 (1-3): 37–48. https://doi.org/10.1007/BF00842902.

Chapman, D.D., M.J. Corcoran, G.M. Harvey, S. Malan, and M.S. Shivji. 2003. Mating behavior of southern stingrays, *Dasyatis americana* (Dasyatidae). *Environmental Biology of Fishes* 68 (3): 241–245.

Clark, E., and K. von Schmidt. 1965. Sharks of the central Gulf coast of Florida. *Bulletin of Marine Science* 15: 13–83.

Collins, A.B., M.R. Heupel, and P.J. Motta. 2007. Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a southwest Florida estuary. *Journal of Fish Biology* 71 (4): 1159–1178. https://doi.org/10.1111/j.1095-8649.2007.01590.x.

Conrath, C.L., and J.A. Musick. 2007. The sandbar shark summer nursery within bays and lagoons of the eastern shore of Virginia. *Transactions of the American Fisheries Society* 136 (4): 999–1007. https://doi.org/10.1577/t06-107.1.

Conrath, C.L., and J.A. Musick. 2012. Reproductive biology of elasmobranchs. In *Biology of sharks & their relatives*, ed. J.C. Carrier, J.A. Musick, and M.R. Heithaus. London: CRC Press.

Cortés, E., C.A. Manire, and R.E. Hueter. 1996. Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in Southwest Florida. *Bulletin of Marine Science* 58: 353–367.

Dedman, S., R. Officer, M. Clarke, D.G. Reid, and D. Brophy. 2017. Gbm.auto: a software tool to simplify spatial modelling and Marine Protected Area planning. *PLoS One* 12 (12): 1–16. https://doi.org/10.1371/journal.pone.0188955.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J.R.G. Marquéz, B. Gruber, B. Lafourcade, P.J. Leitão, T. Münkemüller, C. McClean, P.E. Osborne, B. Reineking, B. Schröder, A.K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1): 027–046. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Driggers, W.B., B.S. Frazier, D.H. Adams, G.F. Ulrich, C.M. Jones, E.R. Hoffmayer, and M.D. Campbell. 2014. Site fidelity of migratory bonnethead sharks *Sphyrna tiburo* (L. 1758) to specific estuaries in South Carolina, USA. *Journal of Experimental Marine Biology and Ecology* 459: 61–69. https://doi.org/10.1016/j.jembe.2014.05.006.

Drymon, J.M., S.P. Powers, J. Dindo, B. Dzwonkowski, and T.A. Henwood. 2010. Distributions of sharks across a continental shelf in the northern Gulf of Mexico. *Marine and Coastal Fisheries* 2 (1): 440–450. https://doi.org/10.1577/C09-061.1.

Drymon, J.M., S. Dedman, J.T. Froeschke, E.A. Seubert, A.E. Jefferson, A.M. Kroetz, J.F. Mareska, and S.P. Powers. 2020. Defining sex-specific habitat suitability for a northern Gulf of Mexico shark assemblage. *Frontiers in Marine Science* 7: 1–18. https://doi.org/10.3389/fmars.2020.00035.

Duncan, K.M., and K.N. Holland. 2006. Habitat use, growth rates and dispersal patterns of *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series* 312: 211–221.

Economakis, A.E., and P.S. Lobel. 1998. Aggregation behavior of the grey reef shark. *Environmental Biology of Fishes* 51 (2): 129–139.

Elith, J., J.R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77 (4): 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Fluharty, D. 2000. Habitat protection, ecological issues, and implementation of the Sustainable Fisheries Act. *Ecological Applications* 10 (2): 325–337. https://doi.org/10.1890/1051-0761(2000)010[0325:HPEIAI]2.0.CO;2.

Froeschke, J.T., G.W. Stunz, B. Sterba-Boatwright, and M.L. Wildhaber. 2010a. An empirical test of the 'shark nursery area concept' in Texas bays using a long-term fisheries-independent data set. *Inter-Research Aquatic Biology* 11 (1): 65–76. https://doi.org/10.3354/ab00290.

Froeschke, J.T., G.W. Stunz, and M.L. Wildhaber. 2010b. Environmental influences on the occurrence of coastal sharks in estuarine waters. *Marine Ecology Progress Series* 407: 279–292. https://doi.org/10.3354/meps08546.

Gelsleichter, J., C.J. Walsh, N.J. Szabo, and L.E.L. Rasmussen. 2006. Organochlorine concentrations, reproductive physiology, and immune function in unique populations of freshwater Atlantic stingrays (Dasyatis sabina) from Florida's St. Johns River. *Chemosphere* 63 (9): 1506–1522.

Grubbs, R.D., J.A. Musick, C.L. Conrath, and J.G. Romine. 2007. Long-term movements, migration, and temporal delineation of summer nurseries for juvenile sandbar sharks in the Chesapeake Bay region. In Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States, ed. C.T. McCandless, N.E. Kohler, and H.L. Pratt Jr., 87–107. Bethesda, MD: American Fisheries Society, Symposium 50.

Guttridge, T.L., S.H. Gruber, B.R. Franks, S.T. Kessel, K.S. Gledhill, J. Uphill, J. Krause, and D.W. Sims. 2012. Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series* 445: 279–291. https://doi.org/10.3354/meps09423.

Henderson, A.C., J.L. McIlwain, H.S. Al-Oufi, S. Al-Sheile, and N. Al-Abri. 2009. Size distributions and sex ratios of sharks caught by Oman's artisanal fishery. *African Journal of Marine Science* 31 (2): 233–239. https://doi.org/10.2989/AJMS.2009.31.2.11.883.

Hendrickson, D., and A. Cohen. 2015. Smalltail shark, *Carcharhinus porosus*. Fishes of Texas project database (version 2.0). http://www.fishesoftexas.org/specimen/USNM196798

Heupel, M.R., and C.A. Simpfendorfer. 2008. Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology* 1: 277–289. https://doi.org/10.3354/ab00030.

Heupel, M.R., and C.A. Simpfendorfer. 2011. Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. *Marine Ecology Progress Series* 433: 237–244. https://doi.org/10.3354/meps09191.

Heupel, M.R., C.A. Simpfendorfer, and R.E. Hueter. 2004. Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes* 71 (2): 135–142. https://doi.org/10.1023/b:ebfi.0000045710.18997.f7.

Heupel, M.R., J.K. Carlson, and C.A. Simpfendorfer. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* 337: 287–297. https://doi.org/10.3354/meps337287.

Heupel, M.R., S. Kanno, A. Martins, and C. Simpfendorfer. 2019. Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Marine and Freshwater Research* 70 (7): 897–907. https://doi.org/10.1071/MF18081.

Hijmans, R.J. 2017. raster: geographic data analysis and modeling. R package version 3.0–12. https://cran.r-project.org/web/packages/raster/index.html

Holland, K.N., B.M. Wetherbee, J.D. Peterson, and C.G. Lowe. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia* 1993 (2): 495–502. https://doi.org/10.2307/1447150.

Hueter, R.E., and J.P. Tyminski. 2007. Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off penisular Florida and Texas. In *Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States*, ed. C.T. McCandless, N.E. Kohler, and H.L. Pratt Jr., 193–224. Bethesda: American Fisheries Society, Symposium 50.

Johnson, M.R., and F.F. Snelson. 1996. Reproductive life history of the Atlantic stingray, *Dasyatis sabina* (Pisces, Dasyatidae), in the freshwater St. Johns River, Florida. *Bulletin of Marine Science* 59: 74–88.

Joung, S.-J., Y.-Y. Liao, K.-M. Liu, C.-T. Chen, and L.-C. Leu. 2005. Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the northeastern waters of Taiwan. *Zoological Studies* 44: 102–110.

Klimley, A. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* 18 (1): 27–40.

Last, P., W.T. White, M.R. de Carvalho, B. Séret, M.F.W. Stehmann, and G.J.P. Naylor. 2016. Dasyatidae (stingrays). In *Rays of the world*, ed. P.R. Last and G.K. Yearsley, 522–618. Clayton South: CSIRO Publishing.

Lessa, R.P., and Z. Almeida. 1998. Feeding habits of the bonnethead shark, *Sphyrna tiburo*, from northern Brazil. *Cybium* 22: 383–394.

Lombardi-Carlson, L.A., E. Cortés, G.R. Parsons, and C.A. Manire. 2003. Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Marine & Freshwater Research* 54 (7): 875–883.

Manire, C., L. Rasmussen, D. Hess, and R.E. Hueter. 1995. Serum steroid hormones and the reproductive cycle of the female bonnethead shark, *Sphyrna tiburo*. *General and Comparative Endocrinology* 97 (3): 366–376. https://doi.org/10.1006/gcen.1995.1036.

Martinez-Andrade, F., M. Fisher, B. Bowling, and B. Balboa. 2012. *Marine resource monitoring operations manual*. Austin: Texas Parks and Wildlife Department.

McCallister, M., R. Ford, and J. Gelsleichter. 2013. Abundance and distribution of sharks in Northeast Florida waters and identification of potential nursery habitat. *Marine and Coastal Fisheries* 5 (1): 200–210. https://doi.org/10.1080/19425120.2013.786002.

McEachran, J.D., and J.D. Fechhelm. 2005. Fishes of the Gulf of Mexico, *volume 2*. Austin: University of Texas Press.

National Geophysical Data Center. 2018. Corpus Christi, Texas 1/3 arc-second MHW coastal digital elevation model. National Atmospheric and Oceanographic Administration. https://catalog.data.gov/dataset/corpus-christi-texas-coastal-digital-elevation-model

Neer, J.A., and B.A. Thompson. 2005. Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* 73 (3): 321–331. https://doi.org/10.1007/s10641-005-2136-5.

NIMA. 2004. *World Geodetic System 1984.* TR8350.2 Third Edition, Amendment 2, 23 June 2004. National Imagery and Mapping Agency, US Department of Defense.

NMFS. 2003. *Final Amendment 1 to the fishery management plan for Atlantic tunas, swordfish, and sharks*. Silver Spring: National Marine Fisheries Service.

Nosal, A.P., E.A. Lewallen, and R.S. Burton. 2013. Multiple paternity in leopard shark (*Triakis semifasciata*) litters sampled from a predominantly female aggregation in La Jolla, California, USA. *Journal of Experimental Marine Biology & Ecology* 446: 110–114.

Oksanen, J., F. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, H. Wagner. 2018. vegan: community ecology package. R package version 2.5–6. https://cran.r-project.org/web/packages/vegan/index.html

Parsons, G.R., and E.R. Hoffmayer. 2005. Seasonal changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the north central Gulf of Mexico. *Copeia* 2005 (4): 914–920.

Parsons, G.R., and E. Hoffmayer. 2007. Identification and characterization of shark nursery grounds along the Mississippi and Alabama Gulf coasts. In *Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States*, ed. C.T. McCandless, N.E. Kohler, and H.L. Pratt Jr., 301–316. Bethesda: American Fisheries Society, Symposium 50.

Pierce, S.J., S.A. Pardo, and M.B. Bennett. 2009. Reproduction of the blue-spotted maskray *Neotrygon kuhlii* (Myliobatoidei: Dasyatidae) in south-east Queensland, Australia. *Journal of Fish Biology* 74 (6): 1291–1308. https://doi.org/10.1111/j.1095-8649.2009.02202.x.

Plumlee, J.D., K.M. Dance, P. Matich, J.A. Mohan, T.M. Richards, T.C. Tinhan, M.R. Fisher, and R.J.D. Wells. 2018. Estuarine, coastal and shelf science community structure of elasmobranchs in estuaries along the northwest Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 204: 103–113. https://doi.org/10.1016/j.ecss.2018.02.023.

R Development Core Team. 2008. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing http://www.r-project.org.

Ramírez-Mosqueda, E., J.C. Pérez-Jiménez, and M. Mendoza-Carranza. 2012. Reproductive parameters of the southern stingray *Dasyatis americana* in southern Gulf of Mexico. *Latin American Journal of Aquatic Research* 40 (2): 335–344.

Seutin, G., B.N. White, and P.T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* 69 (1): 82–90.

Simpfendorfer, C.A., and N.E. Milward. 1993. Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes* 37 (4): 337–345.

Simpfendorfer, C.A., G.G. Freitas, T.R. Wiley, and M.R. Heupel. 2005. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. *Estuaries* 28 (1): 78–85. https://doi.org/10.1007/BF02732755.

Sims, D. 2005. Differences in habitat selection and reproductive strategies of male and female sharks. In *Sexual segregation in vertebrates: ecology of two sexes*, ed. K.E. Ruckstuhl and P. Neuhaus, 127–147. Cambridge: Cambridge University Press.

Snelson, F.F., S.E. Williams-Hooper, and T.H. Schmid. 1988. Reproduction and ccology of the Atlantic stingray, *Dasyatis sabina*, in Florida coastal lagoons. *Copeia* 1988 (3): 729–739.

Stevens, J.D., and K.J. McLoughlin. 1991. Distribution, size and sex composition, reproductive-biology and diet of sharks from northern Australia. *Australian Journal of Marine and Freshwater Research* 42 (2): 151–199.

Stunz, G.W., T. Minello, and P.S. Levin. 2002. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. *Estuaries* 25 (1): 76–85. https://doi.org/10.1007/BF02696051.

Stunz, G.W., T. Minello, and P. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Marine Ecology Progress Series* 406: 147–159.

Thorpe, T., C.F. Jensen, and M.L. Moser. 2004. Relative abundance and reproductive characteristics of sharks in southeastern North Carolina coastal waters. *Bulletin of Marine Science* 74: 3–20.

Tricas, T.C., K.P. Maruska, and L.E.L. Rasmussen. 2000. Annual cycles of steroid hormone production, gonad development, and reproductive behavior in the Atlantic stingray. *General and Comparative Endocrinology* 118 (2): 209–225. https://doi.org/10.1006/gcen.2000.7466.

Ulrich, G.F., C.M. Jones, W.B. Driggers, J.M. Drymon, D. Oakley, and C. Riley. 2007. Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. *American Fisheries Society Symposium* 50: 125–139.

van Etten, J. 2018. gdistance: distances and routes on geographical grids. R package version 1.3–1. https://cran.r-project.org/web/packages/gdistance/index.html

Ward-Paige, C.A., G.L. Britten, D.M. Bethea, and J.K. Carlson. 2015. Characterizing and predicting essential habitat features for juvenile coastal sharks. *Marine Ecology* 36 (3): 419–431. https://doi.org/10.1111/maec.12151.

Plumlee, J.D, and R.J.D. Wells. 2016. Feeding ecology of three coastal shark species in the northwest Gulf of Mexico. Marine Ecology Progress Series 550: 163–174.

White, W.T., and I.C. Potter. 2004. Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. *Marine Biology* 145 (5): 1023–1032. https://doi.org/10.1007/s00227-004-1386-7.

Wiley, T.R., and C.A. Simpfendorfer. 2007. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. *Bulletin of Marine Science* 80: 171–189.

Yates, P.M., M.R. Heupel, A.J. Tobin, and C.A. Simpfendorfer. 2015. Ecological drivers of shark distributions along a tropical coastline. *PLoS One* 10 (4): 1–18. https://doi.org/10.1371/journal.pone.0121346.

Yokota, L., and P. Rosângela. 2006. A nursery area for sharks and rays in Northeastern Brazil. *Environmental Biology of Fishes* 75 (3): 349–360. https://doi.org/10.1007/s10641-006-0038-9.